



## Physical and Chemical Properties of Fruit and Seeds Eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela<sup>1</sup>

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*Pithecia pithecia* and *Chiropotes satanas* are seed predators that eat fruits with hard pericarps. We measured resistance to puncturing and crushing of fruit and seeds eaten by these two pitheciins at two localities: in evergreen rain forest at Raleighvallen-Voltzberg, Surinam, and in tropical dry/transitional moist forest on islands in Guri Lake, Venezuela. Average measurements of pericarp hardness were similar at both sites for fruit eaten by *Chiropotes*, but a higher maximum value was obtained at the rainforest site. *Chiropotes* and *Pithecia* both ate fruits that had harder pericarps than did fruits eaten by *Ateles paniscus*, but crushing resistances of seeds eaten were lower than values for *Ateles*. Thus, both pitheciins selected fruits with hard pericarps and soft seeds, although there were notable intergeneric differences in hardness of fruit ingested. When fruit became scarce, *Pithecia* ate more flowers, while *Chiropotes* continued to eat fruits with hard seed coverings. Chemical analysis of species of seeds eaten by *Pithecia* suggests that they avoided seeds with extremely high tannin levels, though they tolerated moderate tannin levels in combination with high levels of lipids. We propose that sclerocarpic harvesting (the preparation and ingestion of fruit with a hard pericarp) allows pitheciin monkeys to obtain nutritious seeds, with reduced tannins, that are softer than those ingested by other frugivores.

**KEY WORDS:** *Chiropotes*; *Pithecia*; food choice; fruit hardness; diet; sclerocarpic harvesting; seed chemistry; seed predation; tannin.

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## INTRODUCTION

Three widely separated mammalian taxa, the pitheciin primates [tribe Pitheciini (Rosenberger *et al.*, 1990)], peccaries (family Tavassuidae), and squirrels (family Sciuridae), masticate unusually hard food items in Neotropical forests. Peccaries feed on the ground, where [together with brocket deer (Bodmer, 1989)] they probably ingest the hardest available fruit (Kiltie, 1982), while pitheciin primates [together with squirrels (Emmons, 1990)] occupy the major arboreal seed-eating niche among Neotropical mammals. In order to assess the importance to pitheciins of the mechanical property of food hardness, we collected data on the resistance to puncturing and crushing of fruit, nuts, and seeds eaten by the white-faced saki (*Pithecia pithecia*) and the bearded saki (*Chiropotes satanas*) at two localities, Raleighvallen-Voltzberg, Surinam, and islands in Guri Lake, Venezuela.

Living primates in the Tribe Pitheciini include *Pithecia*, *Chiropotes*, and *Cacajao*. These monkeys are primarily frugivorous, as are most Neotropical primates; however, this term fails to distinguish among different strategies of frugivory. Whereas most primate frugivores, such as *Ateles*, eat soft ripe fruit pulp, the three pitheciins are predators on the seeds of fruits that have hard pericarps (Ayres, 1986; van Roosmalen *et al.*, 1988; Kinzey and Norconk, 1990; Kinzey *et al.*, 1990). We present both mechanical and biochemical data from two of these three genera, to determine whether physical and chemical properties of foods influence food choice. While our data support the view that these two pitheciins practice sclerocarpic harvesting—the preparation and ingestion of fruit with a hard pericarp (Kinzey and Norconk, 1990)—and are dentally adapted to opening hard fruit, there are notable intergeneric differences in hardness of fruit ingested.

## METHODS

We conducted the study in Raleighvallen-Voltzberg Nature Reserve in central Surinam (4°41'N, 56°10'W) and at Guri Lake, Bolívar State, Venezuela (7°45'N, 62°52'W). The Surinam site was described previously (Mittermeier and van Roosmalen, 1981; van Roosmalen, 1985). Guri Lake is a reservoir approximately 70 km south of the industrial city of Puerto Ordaz, formed as a result of flooding behind the Raul Leoni Dam on the Caroní River. The 4250-km<sup>2</sup> lake contains more than 100 islands ranging in size from <1 ha to >15 km<sup>2</sup>. We studied *Pithecia* in a small forest patch on a 70-ha island of savanna and tropical dry forest at the northern end

of the lake and *Chiropotes* 40 km to the south on a 365-ha island of transitional tropical moist forest. Both islands also support groups of *Alouatta seniculus* and *Cebus nigritivittatus*. The islands are described in greater detail by Kinzey *et al.* (1988).

The group of *Pithecia* consisted of a pair of adults. The group of *Chiropotes* consisted of 11 independent animals plus 1 carried infant in 1989 and 121 independent animals plus 2 carried infants in 1990. The group of *Chiropotes* in Surinam consisted of 16 animals (Kinzey and Norconk, 1990). All feeding data were obtained on days during which we followed the group all day, from the time animals left their sleeping tree until they reached a tree (or trees) to sleep for the night. We followed animals for at least 2 consecutive days every month; other days were spread across the month. We gathered data during 16 months for *Pithecia*; the data for *Chiropotes* were gathered during 6 months in Surinam and 5 months in Venezuela. We timed the duration of feeding minutes in each feeding tree (from first animal into the tree to last animal leaving) for a total of 10,119 feeding min for *Pithecia*, 3209 feeding min for *Chiropotes* at Guri, and 2086 feeding min for *Chiropotes* in Surinam. Feeding percentages thus represent proportions of feeding time on different foods.

We distinguished three types of frugivory: (i) when *only* seeds were eaten, (ii) when pulp and seeds were eaten together, and (iii) when seeds were discarded uneaten. Sakis also drop many pieces of fruit while feeding. We assume that fruit dropped whole, but with evidence of dental puncture or scraping, indicated an unsuccessful attempt to open it. Seeds still remaining in partially eaten fruit were taken to represent seeds ingested; those in unopened fruit were considered "uneaten."

The hardness of dropped fruit was measured on the same day in the field using instruments described by Kinzey and Norconk (1990). Measurements were not recorded from fruit with evidence of insect damage. Resistance to puncturing of the external covering (pericarp, unless otherwise noted) was measured, and the average of three measurements for each piece of fruit was recorded as kilograms per square millimeter. The resistance of seeds to crushing was measured and recorded as kilograms of force (strength) required to break open the seed. Since the seed is destroyed during crushing, we recorded one value per seed.

The most frequently eaten food resources of *Pithecia* were analyzed biochemically. Leaves and fruit were collected in the field and transported to the United States within 48 hr of collection. Specimens were dried to constant dry weight at 50°C and analyzed by Dr. Nancy Conklin at Harvard University. Total lipid content was measured using petroleum ether extraction for 4 days at room temperature (Association of Official Analytical Chemists, 1984) as modified by Harborne (1984). Water-soluble

carbohydrates were estimated using a phenol/sulfuric acid colorimetric assay (DuBois *et al.*, 1956), as modified by Strickland and Parsons (1972). Condensed tannin content was measured using the proanthocyanidin test of Bate-Smith (1975), as modified by Mole and Waterman (1987). Available protein was estimated using the ninhydrin procedure developed by Marks *et al.* (1987).

Chivers *et al.* (1984) divide the process of feeding or eating into a series of steps. In this paper we are specifically concerned with four of these—selection, ingestion, mastication, and digestion—and we define our terms accordingly. Food selection, or food choice, within certain constraints, is based largely on nutrient content, including both nutrient value and antifeedants (Waterman, 1984). At another time we will discuss food selection in relation to food availability; here we are concerned with what foods the pitheciins select to ingest. Ingestion is “the separation of a bite of food from its matrix for further processing” (Kay, 1984, p. 42), and we use the term specifically to refer to biting into fruit with the canine teeth (and/or incisors or premolars, in some cases) and transfer of the bite into the oral cavity. Mastication (Hiemäe and Kay, 1973) is the chewing or mechanical breakup of food by premolars and molar teeth to increase its surface area in preparation for digestion. Digestion refers to the chemical processing of food in the digestive tract. Thus, a seed that is masticated is (presumably) later digested, but a seed from an ingested fruit that is not masticated usually passes through the digestive tract and is excreted (dispersed) and not digested.

## RESULTS

### Feeding and Foraging of *Pithecia*

Except during January, *Pithecia* spent at least 85% of the feeding time every month eating fruit (Table I). During January the percentage of fruit-feeding time dropped to 71%. Leaves were a small but consistent portion of the diet virtually every day. Every month *Pithecia* ate some insects (mostly ants, but also walking sticks and grasshoppers), though the amount of time spent feeding on insects was never high. They usually spent less time eating insects than leaves on any given day. They also occasionally ate termite nests, but examination of nests revealed that they were usually old and abandoned. *Pithecia* ate significant quantities of flowers only during the dry season, when fruit was scarce (late December to early April).

Table I. Feeding Summary for *Pithecia pithecia* at Guri, Venezuela<sup>a</sup>

Month	N days	Feed min	% fruit						Top two fruit species	
			S	F	% Lf	% In	% Fl	1st	2nd	
Oct. 88	9	936	72	19	7	4	0	<i>Licania</i>	<i>Connarus</i>	
Nov. 88	12	1615	71	14	11	6	0	<i>Licania</i>	<i>Connarus</i>	
Dec. 88	4	238	67	25	4	>1	1	<i>Connarus</i>	<i>Peltogyne</i>	
May 89	6	712	88	3	6	1	>1	<i>Licania</i>	<i>Connarus</i>	
June 89	5	669	68	20	9	2	0	<i>Licania</i>	<i>Connarus</i>	
July 89	5	694	51	36	12	1	0	<i>Connarus</i>	<i>Erythroxylum</i>	
Aug. 89	5	723	44	42	13	1	0	<i>Connarus</i>	<i>Erythroxylum</i>	
Sept. 89	4	264	49	42	9	2	0	<i>Connarus</i>	<i>Erythroxylum</i>	
Oct. 89	5	406	59	30	8	2	0	<i>Connarus</i>	<i>Chiococca</i>	
Nov. 89	4	381	63	29	7	2	0	<i>Chiococca</i>	<i>Connarus</i>	
Dec. 89	4	452	40	51	1	1	6	<i>Capparis</i>	<i>Connarus</i>	
Jan. 90	5	438	49	22	10	>1	15	<i>Piptadenia</i>	<i>Connarus</i>	
Feb. 90	5	488	65	21	7	>1	3	<i>Licania</i>	<i>Piptadenia</i>	
Mar. 90	5	948	68	23	4	2	3	<i>Licania</i>	<i>Connarus</i>	
Apr. 90	5	785	77	18	>1	2	1	<i>Licania</i>	<i>Connarus</i>	
May 90	4	422	38	50	9	>1	>1	<i>Connarus</i>	<i>Chiococca</i>	
Annual Average:			60.6	27.8	7.1	2.3	2.2	<i>Licania</i>	<i>Connarus</i>	

<sup>a</sup>S, seeds only; F, all other fruit; Lf, leaves, In, insects; Fl, flowers. *Licania*, *L. discolor*; *Connarus*, *C. venezuelanus*; *Peltogyne*, *P. floribunda*; *Erythroxylum*, *E. steyermarkii*; *Chiococca*, *C. alba*; *Capparis*, *C. sp. nov.*; *Piptadenia*, *P. leucoxydon*.

*Pithecia* masticated seeds from 39 of 41 identified species of fruit. We failed to find evidence of whole seeds in the pelleted feces we collected, though identifiable insect chitin was visible on gross examination. *Pithecia* discarded intact seeds of *Protium tenuifolium* (Burseraeaceae) and *Strychnos nuxifera* (Loganiaceae); on an annual basis they comprised only 1% of the total fruit-feeding minutes. Thus, 99% of the total fruit-feeding time included ingestion and mastication of seeds and/or seeds together with pulp.

In Table I we divided fruit species into those for which *Pithecia* ate only seeds (17 species) and all others (24 species). Thus, we isolated fruit for which the seed was the primary object of food selection. Exclusive seed-eating comprised 38 to 88% of the feeding time during any month. The top-ranked fruit every month (except November 1989) was in this category. *Licania discolor* (Chrysobalanaceae) and *Conarus venezuelanus* (Connaraceae) provided the majority of seeds masticated during most months. During months when these two species produced few fruits, *Pithecia* ate more flowers and seeds of a variety of other species, increasing their dietary breadth.

#### Feeding and Foraging of *Chiropotes*

Feeding data for *Chiropotes* (Table II) are generally consistent with results that we reported previously from Surinam (Kinzey and Norconk, 1990). *Chiropotes* spent at least 91% of the feeding time each month eating fruit. Leaves, insects, and flowers were rarely eaten: leaves on 3 of 13 days, insects on 6 days, and flowers on 2 days.

*Chiropotes* ate the seeds of 35 of 39 fruit species and discarded the seeds of 4 species. In Table II we divided fruits into those for which *Chiropotes* ate only the seeds (27 species) and all others (12 species). Thus, as for *Pithecia*, we isolated fruit for which the seed was the primary object of food selections. Exclusive seed-eating comprised 52 to 91% of the feeding time during any month. The top-ranked fruit every month was in this category.

#### Hardness Data

##### Puncture Resistance of Fruit Eaten by *Pithecia*

We obtained puncture resistance measurements from 17 species of fruit ingested by *Pithecia* (Table III). The maximum (6.8 kg/mm<sup>2</sup>) was considerably greater than that of any fruit eaten by *Ateles paniscus* (maximum, 1.4 kg/mm<sup>2</sup>) in Surinam but not as hard as the maximum recorded (37.8 kg/mm<sup>2</sup>) for *Chiropotes* in either Surinam or Venezuela (Kinzey and Norconk, 1990). The average value for *Pithecia* (1.20 ± 0.29 kg/mm<sup>2</sup>) was also intermediate between

Table II. Feeding Summary for *Chiropotes satanas* at Guri, Venezuela<sup>a</sup>

Month	N days	Feed min	% fruit		% Lf	% In	% Fl <sup>b</sup>	Top two fruit species	
			S	F				1st	2nd
Sept. 89	3	410	52	44	1	2	0	<i>Brosimum</i>	<i>Protium</i>
Oct. 89	3	908	69	30	<1	1	0	<i>Brosimum</i>	<i>Oryctanthus</i>
Dec. 89	4	1093	91	6	0	2	0	<i>Pradosia</i>	<i>Brosimum</i>
Feb. 90	1	280	64	33	0	0	1	<i>Chrysophyllum</i>	<i>Pradosia</i>
Mar. 90	2	518	75	16	<1	>1	2	<i>Chrysophyllum</i>	Unknown
Average			74.8	21.6	0.2	0.5	0.4	<i>Brosimum</i>	<i>Pradosia</i>

<sup>a</sup> S, seeds only; F, all other fruit; Lf, leaves; In, insects; Fl, flowers. *Brosimum*, *B. alicastrum*; *Pradosia*, *P. caracasana*; *Protium*, *P. neglectum*; *Chrysophyllum*, *C. lucentifolium*; *Oryctanthus*, *O. alveolatus*.

<sup>b</sup> Averages do not add to 100% because some food items were not identified.

Table III. Puncture Resistance of Fruit Eaten by *Pithecia pithecia* During August 1988-May 1990, Guri, Venezuela<sup>a</sup>

Species	Family	N	kg/mm <sup>2</sup>		
			Min	Ave.	Max.
<i>Agonandra brasiliensis</i>	Opiliaceae	1	0.81	0.81	0.81
<i>Alouatta corymbosa</i>	Rubiaceae	1	0.67	0.67	0.67
<i>Angostura trifoliata</i>	Rutaceae	5	0.56	0.90	1.06
<i>Araibidaea</i> sp.	Bigoniaceae	2	0.57	0.98	1.38
<i>Capparis</i> sp. nov.	Capparidaceae	23	0.81	2.74	5.02
<i>Chiococca alba</i>	Rubiaceae	1	0.01	0.01	0.01
<i>Chrysophyllum argenteum</i>	Sapotaceae	3	0.15	0.28	0.37
<i>Chrysophyllum lucenifolium</i> <sup>b</sup>	Sapotaceae	8	0.81	1.19	1.89
<i>Chrysophyllum lucenifolium</i> <sup>c</sup>	Sapotaceae	4	4.70	5.20	5.73
<i>Coccoloba latifolia</i>	Polygonaceae	1	1.15	1.15	1.15
<i>Connarus venezuelanus</i>	Connaraceae	52	0.35	0.91	2.25
<i>Licania discolor</i>	Chrysobalanaceae	74	0.56	2.97	6.77
<i>Maytenus guianensis</i>	Celastraceae	2	0.67	0.68	0.69
<i>Peltogyne floribunda</i>	Caesalpiniaceae	8	0.46	0.82	1.18
<i>Pipiadenia leucoxylon</i>	Mimosaceae	5	0.29	0.63	1.82
<i>Pipiadenia peregrina</i>	Mimosaceae	1	0.93	0.93	0.93
<i>Psidium sartorianum</i>	Myrtaceae	2	0.10	0.14	0.19
(Unknown) pod	Bigoniaceae	5	0.45	0.61	1.04
Range		198	0.01		6.77
Average of 17 species ( $\bar{X} \pm SE$ )				1.20 $\pm$ 0.29	

<sup>a</sup> N, number of specimens; min., minimum value recorded; max., maximum value recorded; ave., average of values for each species.

<sup>b</sup> Picked from the tree.

<sup>c</sup> Picked up from the ground.

the average for *Ateles* ( $0.54 \pm 0.07$  kg/mm<sup>2</sup>) and the average for *Chiropotes* ( $2.15 \pm 0.37$  kg/mm<sup>2</sup>). It appears that *Pithecia* do indeed ingest hard fruit, but that which is less hard than fruit ingested by *Chiropotes*.

Fruit of *Connarus* and *Licania* dropped unopened had softer pericarp than opened fruit whose seeds had been eaten, though the difference was not significant for the dehiscent *Connarus* (Table IV). Increased pericarp hardness may have signaled improved nutrient content and/or reduced secondary compounds such as tannin.

#### Puncture Resistance of Fruit Eaten by *Chiropotes*

We obtained puncture resistances from 24 species of fruit eaten by *Chiropotes* in Venezuela (Table V). The maximum value was 7.2 kg/mm<sup>2</sup>

Table IV. Puncture Resistance of Fruit Eaten or Not Eaten by *Pithecia pithecia*, August 1988-May 1990, Guri, Venezuela

	N	Puncture resistance of pericarp (kg/mm <sup>2</sup> )	
		Mean $\pm$ SE	Range
<i>Connarus</i>			
Ripe (eaten)	52	0.91 $\pm$ 0.65	0.35-2.25
Unripe (not eaten)	5	0.55 $\pm$ 0.05	0.45-0.71
<i>Licania</i>			
Ripe (eaten)	74	2.97 $\pm$ 0.18	0.56-6.77
Unripe (not eaten)	14	1.71 $\pm$ 0.30	0.91-3.79
Ripe <sup>a</sup>	14	4.35 $\pm$ 0.25	3.08-6.32

<sup>a</sup> Dropped by *Alouatta seniculus*; only mesocarp eaten.

for a pod from an unknown species of Bigoniaceae. Bignon pod appear to be an important food resource during the dry season, so during lean times *Chiropotes* may rely on hard fruit that other animals are unequipped to open. These data are generally comparable to those we collected previously in Surinam (Fig. 1), though it is clear that even the toughest bignone pod eaten in Venezuela is nearly an order of magnitude softer than *Licania majuscula* (Chrysobalanaceae) eaten in Surinam ( $37.8$  kg/mm<sup>2</sup>). The average value of fruit hardness from Venezuela ( $2.32 \pm 0.40$  kg/mm<sup>2</sup>) is not significantly different from that obtained in Surinam ( $2.01 \pm 0.61$  kg/mm<sup>2</sup>), and the combined average value is  $2.15 \pm 0.37$  kg/mm<sup>2</sup> ( $N=53$  species).

#### Crushing Resistance of Seeds

Crushing resistances of 17 species of seeds eaten by *Pithecia* are given in Table VI. The hardest seeds were those of *Coccoloba latifolia* (Polygonaceae)—up to 37.0 kg. The small fruit of *Coccoloba* (<1-cm diameter) were eaten whole, including adherent testa. The average value of seeds eaten by *Pithecia* ( $8.76 \pm 2.13$  kg) was intermediate in hardness between those eaten by *Chiropotes* ( $4.63 \pm 0.55$  kg in Venezuela,  $6.63 \pm 1.35$  kg in Surinam) and those swallowed whole by *Ateles* ( $21.16 \pm 7.22$  kg) (Kinzey and Norconk, 1990). Seasonal differences in pericarp hardness will be reported elsewhere.

Table V. Puncture Resistance of Fruit Eaten by *Chiropotes satanas* During September 1989–May 1990, Guri, Venezuela<sup>a</sup>

Species	Family	N	kg/mm <sup>2</sup>		
			Min.	Avc.	Max.
<i>Amphitophium</i> sp. 1	Bignoniaceae	1	1.08	1.08	1.08
<i>Amphitophium</i> sp. 2	Bignoniaceae	3	1.11	1.19	1.31
<i>Apeiba schomburgkii</i>	Tiliaceae	1	1.04	1.04	1.04
<i>Brosimum alicastrum</i>	Moraceae	13	0.13	0.44	1.28
<i>Byrneria catalpifolia</i>	Sterculiaceae	1	5.88	5.88	5.88
<i>Callihamys</i> sp.	Bignoniaceae	4	1.68	2.70	3.10
<i>Chrysophyllum lucentifolium</i>	Sapotaceae	13	1.08	1.28	1.52
<i>Distictella</i> sp.	Bignoniaceae	2	2.69	2.90	3.10
<i>Luehea speciosa</i>	Tiliaceae	3	3.18	3.56	3.84
<i>Maclura tinctoria</i>	Moraceae	1	0.05	0.05	0.05
<i>Pradosia caracasana</i>	Sapotaceae	19	0.16	1.14	2.19
<i>Protium neglectum</i>	Burserraceae	5	0.51	0.61	0.78
Species A	Bignoniaceae	9	1.53	3.30	4.26
Species B	Bignoniaceae	6	4.35	5.09	6.33
Species C	Bignoniaceae	1	5.34	5.34	5.34
Species D	Bignoniaceae	3	1.06	2.49	3.54
Species E	Bignoniaceae	2	6.38	6.78	7.18
Species F	Bignoniaceae	6	1.52	2.55	4.19
Species G	Bignoniaceae	4	3.72	4.10	4.51
Unknown	Leguminosae	1	1.16	1.16	1.16
Unknown	Moraceae	4	1.03	1.12	1.20
Species A	Sapotaceae	4	0.10	0.19	0.25
Species B	Sapotaceae	6	1.53	1.69	1.92
"Liana fruit"	Unknown	2	0.05	0.05	0.05
Range		115	0.05		7.18
Average of 24 species ( $\bar{X} \pm SE$ )				2.32 ± 0.40	

<sup>a</sup> N, number of specimens; min., minimum value recorded; max., maximum value recorded; avc., average of values for each species.

Crushing resistances of seeds of 12 species eaten by *Chiropotes* in Venezuela are presented in Table VII. The average and maximum values are less than values previously reported for *Chiropotes* in Surinam (Kinzey and Norconk, 1990) or for *Pithecia* in Venezuela (Table VI). Seeds masticated by *Chiropotes* are "soft" compared with seeds masticated by *Pithecia* and especially soft compared with those swallowed whole by *Ateles*.

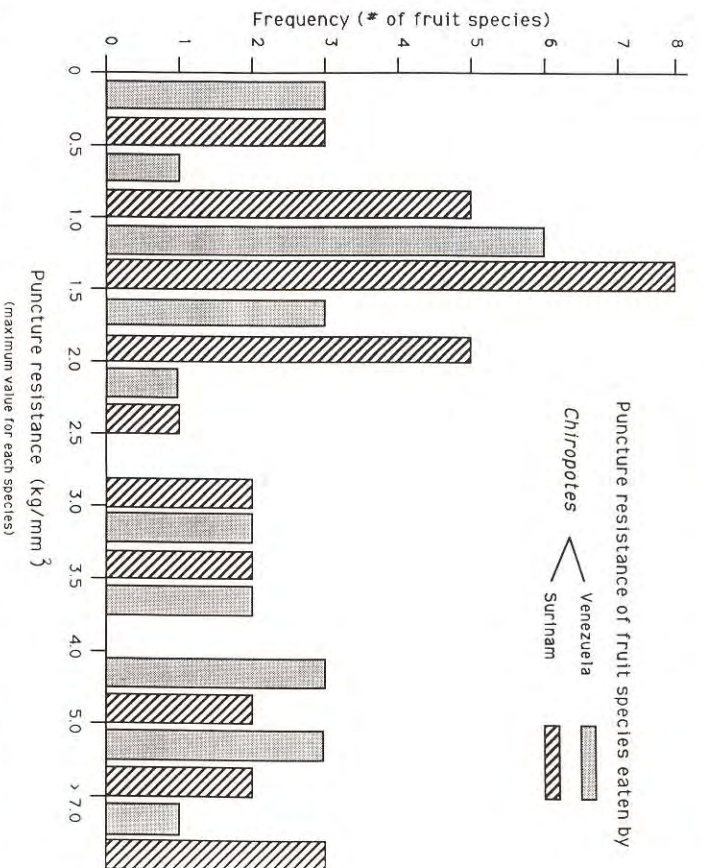


Fig. 1. Distribution of maximum puncture resistance values of the pericarp of fruit species eaten by *Chiropotes satanas* in Surinam and in Venezuela.

Seeds from pieces of fruit eaten by both *Pithecia* and *Chiropotes* have significantly reduced crushing resistances compared with those from whole fruit dropped uneaten (Table VIII). Thus, both sakis appear to select individual fruits with softer seeds. *Pithecia* even go to the ground and pick up and eat *Chrysophyllum lucentifolium* (Sapotaceae) fruit with softer seeds than those obtainable from fruit in the tree.

### Biochemical Data

Seventeen sets of biochemical analyses of six species of fruit eaten by *Pithecia pithecia* in Venezuela are presented in Table IX, which emphasizes the two most frequently eaten food species (Table I), *Licania discolor* and *Conarus venezuelanus* (Kinzey *et al.*, 1990). Extremely high tannin levels were avoided by *Pithecia*; however, moderate levels as high as 9.9%

**Table VI.** Crushing Resistance (kg) of Seeds of Species of Fruit Eaten by *Pithecia pithecia* During September 1988-May 1990, Guri, Venezuela

Species	Family	N	Mean	Min.	Max
<i>Argostura trifoliata</i>	Rutaceae	5	0.8	0.5	1.4
<i>Eugenia</i> sp. 1	Myrtaceae	3	1.3	1.0	2.0
<i>Peltogyne floribunda</i>	Caesalpiniaceae	1	1.8	1.8	1.8
<i>Chiococca alba</i>	Rubiaceae	3	2.0	2.0	2.0
<i>Erythroxylum gracilipes</i>	Erythroxylaceae	21	2.7	1.4	3.2
<i>Erythroxylum steyermarkii</i>	Erythroxylaceae	2	2.8	2.3	3.2
<i>Dioclea guianensis</i>	Papilionaceae	1	4.5	4.5	4.5
<i>Guettarda malacophylla</i>	Rubiaceae	19	4.9	2.7	7.3
<i>Licania discolor</i>	Chrysobalanaceae	23	5.1	2.0	10.0
<i>Eugenia</i> sp. 2	Myrtaceae	3	7.0	3.6	9.1
<i>Actinostemon schomburgkii</i>	Euphorbiaceae	5	7.6	4.1	10.7
<i>Capparis</i> sp. nov.	Capparidaceae	4	7.8	4.5	12.7
<i>Pipadentia leucocylon</i>	Mimosaceae	7	8.6	4.1	20.4
<i>Chrysophyllum lucentifolium</i> <sup>a</sup>	Sapotaceae	2	9.5	9.0	10.0
<i>Psidium sartorianum</i>	Myrtaceae	20	14.5	9.5	18.1
<i>Connarus venezuelanus</i>	Connaraceae	25	15.3	10.0	26.0
<i>Chrysophyllum lucentifolium</i> <sup>b</sup>	Sapotaceae	8	29.6	23.6	36.3
<i>Coccoloba latifolia</i>	Polygonaceae	13	32.0	28.0	37.0
Total		165		0.5	37.0
Average of 17 species ( $\bar{X} \pm SE$ )				8.76 $\pm$ 2.13	

<sup>a</sup> *Pouteria* picked up from the ground.

<sup>b</sup> *Pouteria* dropped from the tree.

(in *Licania*) were tolerated. The mesocarp of *Licania* was avoided by *Pithecia* (even though it was easily scraped from the outside of ripe fruit by *Alouatta*), is high in water-soluble carbohydrate and has a slightly lower tannin level than the ripe seed. We have not observed *Alouatta* to break open the hard shell (endocarp) of *Licania discolor*.

*Pithecia* avoided the green unripe capsules of *Connarus venezuelanus* when red ripe capsules were available in the same tree. Like those of *Licania discolor*, ripe seeds are high in lipid content and have lower tannin levels than unripe seeds. The seed coat of *Connarus* is especially high in lipid, and *Pithecia* usually ate it together with the seed. In addition, fruits of *Connarus* are available in variable abundance year-round (Norconk and Kinzey, 1990). These two top-ranked feeding sources are much higher in lipid content than other, more seasonal, fruits: *Erythroxylum*, *Chiococca*, *Chrysophyllum*, and *Capparis* (Table IX).

We occasionally saw *Pithecia* feed on termite nests. Chemical analysis of nest material eaten by *Pithecia* revealed relatively high iron levels (10%).

**Table VII.** Crushing Resistance (kg) of Seeds of Species of Fruit Eaten by *Chiropotes satanas* During September 1989-May 1990, Guri, Venezuela

Species	Family	N	Mean	Min.	Max.
<i>Brossimum alicastrum</i>	Moraceae	1	0.5	0.5	0.5
<i>Chrysophyllum lucentifolium</i>	apotiaceae	2	2.1	2.0	2.2
<i>Zanthoxylum martinicensis</i>	Rutaceae	10	3.6	0.1	5.0
<i>Cecropia peltata</i>	Moraceae	2	4.3	2.7	5.9
<i>Sapium abietanum</i>	Euphorbiaceae	3	4.8	3.6	6.4
(Unknown species "a")		1	4.8	4.8	4.8
<i>Allophylus occidentalis</i>	Sapindaceae	6	4.9	4.5	5.4
(Unknown)	Leguminosae	1	5.0	5.0	5.0
<i>Lepidocordia punctata</i>	Boraginaceae	10	5.4	3.6	6.8
<i>Pradosia caracasana</i>	Sapotaceae	1	5.9	5.9	5.9
<i>Paullinia cururu</i>	Sapindaceae	1	6.8	6.8	6.8
(Unknown)	Sapotaceae	3	7.5	6.6	9.1
Total		41		0.5	9.1
Average of 12 species ( $\bar{X} \pm SE$ )			4.63 $\pm$ 0.55		

The biochemical data, together with hardness measurements, may explain why *Pithecia* come to the ground to obtain seeds of *Capparis* and *Chrysophyllum*. Both are higher in protein than *Licania* and *Connarus* and produce fruit seasonally. As shown in Tables III and VI, the coverings of these fruits become harder after they have lain on the ground, while the seed, which must be crushed by the molars, becomes softer.

## DISCUSSION

Virtually every month *Pithecia pithecia* and *Chiropotes satanas* spend at least 85% of their feeding time eating fruit. They are seed predators, spending 95-99% of their fruit-feeding time eating fruit whose seeds they digest. At least 38% of feeding time every month is devoted to eating seeds exclusively (Tables I and II). Both sakis eat some insects (mostly ants) every month but not every day (present data; Ayres and Nessimian, 1982; Mittermeier *et al.*, 1983). Both pitheciins are "sclerocarpic foragers" (Kinzey and Norconk, 1990), since much of the fruit they eat has a hard pericarp—harder than that of the hardest fruit eaten by *Ateles*. These dietary differences are related to dental morphology (Kinzey 1987, 1988, 1992; Kinzey and Norconk, 1988, 1990; Rosenberger, 1992). The crushing resistance of seeds is a different issue from pericarp hardness.

Table VIII. Comparison of Crushing Resistance of Seeds Eaten and Not Eaten, Guri, Venezuela<sup>a</sup>

	Average crushing resistance, seeds (kg)			
	Eaten		Not Eaten	
	N	$\bar{X} \pm SE$	N	$\bar{X} \pm SE$
<i>Connarus venezuelanus</i> (P)	24	15.3 ± 0.9	6	30.7 ± 2.5**
<i>Licania discolor</i> (P)	23	5.1 ± 0.5	4	9.2 ± 1.5*
<i>C. lucentifolium</i> (P)				
On ground	2	9.5 ± 0.5	4	—
In tree <sup>b</sup>	8	29.6 ± 1.7	4	46.8 ± 1.4**
<i>Chrysophyllum lucentifolium</i> (Ch)	2	2.1 ± 0.1	9	22.6 ± 1.1*
<i>Brosimum alicastrum</i> (Ch)	1	0.5	1	4.5
<i>Zanthoxylum martinicensis</i> (Ch)	10	3.6 ± 0.4	11	11.8 ± 1.1**

<sup>a</sup> P, *Pithecia*; Ch, *Chiropotes*.

<sup>b</sup> These *Chrysophyllum* were dropped from the tree partly eaten. Those preferred (eaten) were picked up from the ground.

\* Values of seeds eaten significant from those not eaten ( $P < 0.01$ ).

\*\* Values of seeds eaten significant from those not eaten ( $P < 0.001$ ).

Based on considerations presented in detail by Rosenberger and Kinzey (1976), we suggest that sclerocarpic harvesting allows saki monkeys to obtain nutritious seeds that are softer than those swallowed by other frugivores (Kinzey and Norconk, 1990). The following data support this view. (1) *Pithecia* eat fruit whose pericarp has a higher (average and maximum) puncture resistance than fruit dropped unopened (Table IV). (2) Both *Chiropotes* and *Pithecia* masticate seeds whose average crushing resistance is significantly less than that of seeds from fruit they intentionally discard (Table VIII). (3) Both species of saki masticate seeds whose (average and maximum) crushing resistance is significantly less than that of seeds ingested by *Ateles* (Table X). (4) Both *Pithecia* and *Cebus* break open the hard pericarp of *Capparis* sp. nov. with their canine teeth, but seeds representing those masticated by *Cebus* are significantly harder [ $N = 4$ ;  $\bar{X} = 17.9 \pm 1.5$  kg (unpublished data)] than those masticated by *Pithecia* [ $N = 4$ ;  $\bar{X} = 7.83 \pm 1.74$  kg (Table VI)]. Thus, both sakis select fruits which, even though hard, have soft seeds (Fig. 2).

Predation by animals on immature seeds is common (Janzen, 1971) and appears to be typical of primate seed predators [e.g., colobus (Harrison and Hladik, 1986), banded and red leaf-monkeys (Davies *et al.*, 1988), proboscis monkey (Yeager, 1989), and orangutan (Leighton, 1993)]. However, our observations of saki monkeys, especially *Pithecia*, indicate that a substantial portion of seeds is taken from fruit that is ripe or nearly ripe. All unripe seeds that we have tested thus far are high in condensed tannins (Table IX).

Table IX. Biochemical Analyses of Species of Fruit Eaten by *Pithecia pithecia*, Guri, Venezuela

	Percentage		
	Lipid	Protein	CHO <sup>a</sup> Condensed tannins
<i>Licania discolor</i>			
Unripe seeds — not eaten	17.3	5.7	12.6
	1.0	4.3	7.9
	0.0	4.7	7.3
Ripe Seeds — eaten	49.7	4.6	2.2
	49.8	5.2	1.4
Mesocarp (ripe fruit) <sup>b</sup>	2.5	7.0	19.4
<i>Connarus venezuelanus</i>			
Unripe seeds — not eaten	—	—	—
Ripe seeds + seed coat	48.8	8.6	3.8
	48.7	9.3	3.0
	47.9	9.7	3.8
	47.7	4.5	3.1
Seed only (no seed coat)	27.9	8.9	3.9
Seed coat only	64.2	10.6	4.3
<i>Erythroxylum gracilipes</i> , whole fruit, incl. seed	15.6	9.2	9.3
<i>Chiococca alba</i> , whole fruit, incl. seed	4.9	11.3	31.0
<i>Chrysophyllum lucentifolium</i> , seeds	9.0	13.7	24.9
<i>Capparis</i> sp. nov., seeds	8.2	35.0	11.5

<sup>a</sup> Water-soluble carbohydrates (including sugars).

<sup>b</sup> Mesocarp is eaten by *Alouatta* but not by *Pithecia*.

Biochemical measures of preferred fruit indicate that *Pithecia*'s preference for soft seeds may be based on improved nutrient value (Table IX). The two most frequently eaten fruits, *Licania* and *Connarus*, available most months, comprise 49% of the total fruit-feeding time. Both have a high (47–50%) lipid content. Although the protein content of masticated and discarded seeds of *Licania* does not differ, masticated seeds have higher lipid and reduced tannin values compared with discarded seeds. Although extremely high levels of tannin ( $\geq 27\%$ ) were avoided, moderate tannin levels, as high as 9.9% in *Licania*, were tolerated and, perhaps, were offset by the high lipid content in these ripe seeds. This suggests that *Pithecia* are able to detoxify fruits with moderately high tannin levels and/or are willing to accept a tannin tradeoff for seeds with a high fat content.



Table X. Summary of Fruit Hardness

	Puncture resistance of pericarp (kg/mm <sup>2</sup> )		Crushing resistance of seeds (kg)			
	Max. value	$\bar{X} \pm SE$	N	Max. value		
<i>Ateles</i>	19	1.4	0.54 ± 0.07	13	148.2	21.16 ± 7.22
<i>Pithecia</i>	17	6.8	1.20 ± 0.29*	17	37.0	8.76 ± 2.13*
<i>Chiropotes</i>	24	7.2	2.32 ± 0.40**	12	9.1	4.63 ± 0.55*
C. (Surinam)	29	37.8	2.01 ± 0.61*	19	22.3	6.63 ± 1.35*

\*Significantly different from value for *Ateles* ( $P < 0.05$ ).

\*\*Significantly different from value for *Ateles* ( $P < 0.001$ ).

The two next most frequently eaten fruits (*Eythroxyllum* and *Chiococca*), together comprising 13% of the total fruit-feeding time, are highly seasonal and both are very low in condensed tannins. Their protein content is high, though lipid appears to be lower than in *Licania* or *Connarus*. Seasonal fruits, including *Chrysophyllum* and *Capparis*, which are frequently eaten from the ground, may be selected because of their high protein content.

Although *Pithecia pithecia* and *Chiropotes satanas* are both sclerocarpic foragers, our data indicate differences between them. *Chiropotes* eat fewer leaves, not virtually every day as do *Pithecia*, and during the dry season *Pithecia* eat more flowers. On the other hand, during the dry season *Chiropotes* eat more hard fruit, such as *Chrysophyllum* sp. (Sapotaceae), *Licania*, and bignone pods. Maximum pericarp hardness is also greater for fruit eaten by *Chiropotes* than by *Pithecia* (Table X).

*Pithecia* appear to be more versatile feeders than bearded sakis. For example, *Chrysophyllum lucentifolium* (Sapotaceae) is a fruit selected at more than one stage of ripeness. *Pithecia* pick fruits with very hard seeds but appear not to prefer them to those obtained from the ground, which have softer seeds. When *Pithecia* pick *Chrysophyllum* from the tree, they more frequently ingest mesocarp, but even picked and partially eaten fruits have softer seeds than those picked and dropped unopened (Table VIII). *Pithecia* frequently come to the ground to obtain fallen fruit whose seeds have a lower resistance to crushing, even though the fallen fruit has a higher resistance to puncturing (Table III vs. VI). They appear to be selecting soft seeds at the expense of having to penetrate their harder coverings. It appears from our data, at least for the majority of fruit species, that an inverse correlation exists between pericarp and seed hardness.

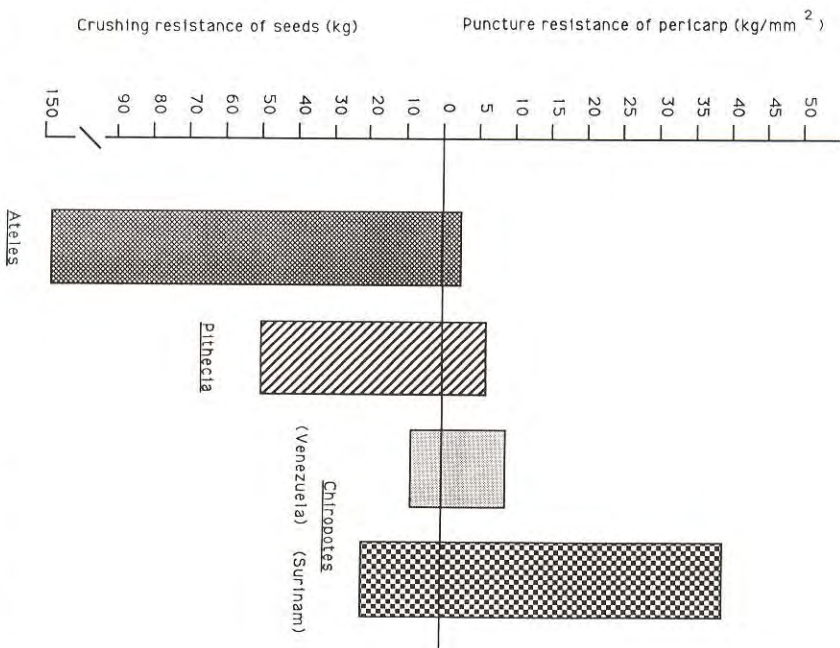


Fig. 2. Comparison of hardness of fruit eaten (maximum values) by *Ateles paniscus* and *Chiropotes satanas* in Surinam and by *Pithecia pithecia* and *Chiropotes satanas* in Venezuela. Hardness is expressed as puncture resistance (kg/mm<sup>2</sup>) of the pericarp and as crushing resistance (kg) of seeds.

Our feeding data on *Pithecia pithecia* are consistent with those from briefer studies. Using data obtained from census walks in Surinam, Mittermeier & van Roomalen (1981) reported that they ate 93.3% fruit (of which 36% were seeds), 6.7% flowers, and no leaves. Using spot observations in northern Brazil, Oliveira *et al.* (1985) reported 79% fruit (of which 22% were immature seeds), 14% flowers, and the remainder leaves and shoots. The higher values (Table I) that we obtained for seed predation may be the result of the dry forest habitat in which we studied *Pithecia*. There are probably fewer fleshy fruit in this forest than in the tropical moist forests of other studies. This

supports previous observations that *Pithecia* are able to survive in a wider variety of habitats than *Chiropotes* are (Muckenhiem *et al.*, 1975; Mittermeier and van Roosmalen, 1981; Kinzey *et al.*, 1988).

Our data for *Chiropotes satanas* (91–99% fruit, of which 52–91% was seeds) (Table II) are similar to those obtained by van Roosmalen *et al.* (1988), based on 217 feeding observations in Surinam over 2.5 years: 96.2% fruit (of which 69% was seeds) and 3.4% flowers. They did not observe insect consumption or leaf-feeding, except as one case of feeding on a young leaf petiole. Based on 189 feeding records obtained over 3 months, Ayres (1981) reported 72.6% fruit (of which 87% was seeds), 11.4% flowers, 11.3% bark or stems, less than 5% leaves, and some insects.

We could not find live termites on any of the termite nests upon which *Pithecia* fed. In the absence of termites, *Pithecia* was probably eating nest substance for its high mineral content, instead of searching for termites. Izawa (1993) also reported high levels of iron, as well as several other minerals, in termite nest material eaten by *Alouatta seniculus* in Colombia. He also suggested that *Alouatta* ate termitaria and soil for mineral supplementation.

For both species of saki monkey, reported variations in feeding habits are probably due to seasonal and habitat differences. At her site in tropical moist forest in Brazil, Setz (1987) found seasonal changes in the diet of *Pithecia pithecia* similar to those we found at Guri: a drop from 77% fruit in wet season to 55% in the dry season, an increase in leaves from 19% wet season to 32% dry season, and an increase in flowers from 0% wet season to 11% dry season. Ayres (1981) did not report seasonal data for *C. satanas*, but he found that *C. albinasus* ate more seeds during the dry season, while eating less fruit mesocarp.

We have yet to measure foods of *Cacajao*, but Ayres (1986) found the highest-ranking plant family in the diet of *C. c. calvus* to be Lecythidaceae (17%), characteristically a family of hard-husked fruit. Like *Pithecia*, *C. c. calvus* also preferred seeds with a high fat content and avoided high levels of condensed tannins, but ate fruit with moderate tannin levels not tolerated by sympatric squirrel monkeys (Ayres, 1986).

Ayres (1989, p. 698) stated that *Cacajao* and *Chiropotes* are unlikely to be sympatric because they "are both frugivores specialized in seed predation." Yet *Chiropotes* and *Pithecia* are broadly sympatric throughout most of their range. They are known to occupy different levels of the canopy in *terra firme* forest (Mittermeier and van Roosmalen, 1981). Our data show that they also differ in the extent of seed predation and the manner in which they cope with depressed fruit availability in the dry season. Thus, while the two larger, sclerocarpic foraging pitheciins, *Chiropotes* and *Cacajao*, are allopatric and eat fruits with very hard pericarps, the smaller *Pithecia*,

which are capable of surviving in a greater variety of habitats and feed on fruits with softer pericarps, are sympatric with both.

Understanding sclerocarpic foraging in the pitheciin primates depends on knowledge of both chemical and physical properties of foods. Since plants protect seeds, mechanically and/or chemically, pitheciins must contend with these protective mechanisms. The two larger genera appear to invest heavily in the ability to thwart the mechanical protection of hard seeds. *Pithecia*, on the other hand, has opted for an intermediate mode, challenging both mechanical protection (but not the hardest coverings) and chemical protection (but only moderate levels of condensed tannins; CT). Seeds eaten by *Pithecia*, that we have analyzed, exchange chemical for physical protection as they mature, but this is not always the case. Seeds of *Cheilochium cognatum* (Celastraceae), eaten by *Cacajao*, for example, decrease in covering hardness and increase in CT content as they mature (Ayres, 1986, p. 200). Thus, the relationship between seed coat hardness/CT and maturation is complex. Sclerocarpic foraging is an effective adaptation for all pitheciin primates to obtain nutritious seeds, but its precise relationship to seed protection and maturation is not yet fully understood.

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